

**Abstract.**— The stomach contents of 1,215 anadromous alewives collected during winter and summer groundfish research surveys (1990–91) off Nova Scotia were examined to 1) describe the diet by season, area, bottom depth (<101 m, 101–200 m, >200 m), time of day and fish size (<151 mm, 151–200 mm, 201–250 mm, >250 mm FL), 2) evaluate diel feeding periodicity, and 3) estimate daily ration. Euphausiids, particularly *Meganyctiphanes norvegica*, were the most important prey and represented more than 82% by volume of total stomach contents seasonally and geographically. Contributions by other prey groups (hyperiid amphipods, calanoid copepods, crustacean larvae, polychaetes, chaetognaths, mysids, pteropods, and fish larvae) were small and varied temporally and spatially. The proportion of euphausiids in the diet of alewives from the Scotian Shelf (winter) and Bay of Fundy (summer) tended to increase with increasing depth. Day and night differences in diet composition indicate that alewives may particulate-feed on macrozooplankton when prey visibility is high and filter-feed on microzooplankton when prey visibility is low. Diet composition was relatively homogenous among alewife size groups with euphausiids composing most of the total food volume. Alewives of different size groups ate similarly sized *M. norvegica*, generally the largest *M. norvegica* available. Diel feeding activity (stomach fullness) peaked at mid-day (summer collections) and mid-afternoon (winter collections); feeding activity was reduced at night. In all areas, feeding activity and the proportion of feeding fish was highest in regions where bottom depths exceeded 200 m. Mean stomach fullness was highest during summer in the Bay of Fundy and during winter on the Scotian Shelf; these regions are seasonally important foraging areas for alewives off Nova Scotia. Daily ration was 1.2% of body weight during winter and 1.9% during summer.

## Feeding habits of anadromous alewives, *Alosa pseudoharengus*, off the Atlantic Coast of Nova Scotia

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The anadromous alewife, *Alosa pseudoharengus*, is a clupeiform fish whose range extends from Newfoundland to North Carolina (Bigelow and Schroeder, 1953). Off Nova Scotia, alewives occur throughout the year in regions characterized by strong tidal mixing and upwelling in the Bay of Fundy-eastern Gulf of Maine and are abundant during spring in the warmer, deeper waters of the central Scotian Shelf and areas of warm slope water intrusion along the Scotian Slope and the edges of Georges Bank (Stone and Jessop, 1992). In the Maritime provinces of Canada and Atlantic coastal United States, alewives and blueback herring, *A. aestivalis*, are fished commercially during their spring spawning migrations and are often marketed together as gaspereau or river herring. Little is known about the importance of alewives as predators in the marine environment or about their feeding habits and food consumption rates.

Alewives are generally classified as size-selective, particulate and filter-feeding microphagists and can actively feed on individual zooplankton or passively feed by filtering the water with their gill rakers (Janssen, 1976; Durbin, 1979; James, 1988). Feeding mode

depends on prey density, size, and visibility, and on predator size (Janssen, 1976, 1978a, 1978b; Durbin, 1979). The ability to switch feeding modes enables alewives to consume a wide size range of prey in a variety of environmental conditions. Size-selective predation by juvenile and nonanadromous freshwater alewives can shift the species and size composition of zooplankton communities towards smaller forms (Brooks and Dodson, 1965; Brooks, 1968; Wells, 1970; Warsaw, 1972; Vigerstad and Cobb, 1978). No information is available on size-selective predation in the ocean; however, in Minas Basin, a turbid macrotidal estuary, alewives were generally particulate feeders of larger, benthic prey rather than smaller pelagic prey (Stone and Daborn, 1987).

Information on the feeding habits of anadromous alewives in the ocean is limited to qualitative assessments but is better known for freshwater juveniles (Vigerstad and Cobb, 1978; Gregory et al., 1983; Jessop, 1990) and estuarine resident subadults during summer (Stone and Daborn, 1987). Euphausiids, calanoid copepods and, to a lesser extent, hyperiid amphipods, chaetognaths, mysids, pteropods, decapod larvae, and salps

have been identified as prey for alewives in continental shelf waters from North Carolina to Nova Scotia (Holland and Yelverton, 1973; Edwards and Bowman, 1979; Neves, 1981; Vinogradov, 1984; Bowman, 1986). However, none of these studies were comprehensive.

We examined the stomach contents of anadromous alewives obtained from winter and summer groundfish research surveys on the Scotian Shelf, Georges Bank, and in the Bay of Fundy to determine the importance of these regions as foraging areas for these fish. Seasonal, spatial, diel and size-related variability in feeding are examined. Daily ration is estimated from information on diel feeding periodicity.

## Materials and methods

### Data collection

Alewives were collected from seven groundfish research surveys conducted by the Canadian Department of Fisheries and Oceans in three regions (Georges Bank, central Scotian Shelf, and outer Bay of Fundy) during winter (February–March) and summer (July) over a two-year period (1990–91) (Table 1). All surveys used a Western IIA bottom trawl with a 10-mm stretched-mesh liner in the cod end. Thirty-minute tows at each sampling station were conducted throughout the 24-hour day. Up to 40 fish of representative size range from each set were frozen for later analysis. Bottom water temperature (°C), time of tow deployment, latitude, longitude, and bottom depth (m) were recorded for each set. Stomach content data were grouped by season and sample location: Winter-Fundy, Winter-Shelf, Winter-Georges, and Summer-Fundy (Fig. 1). Stone

and Jessop (1992) provide additional details of the survey area and procedures, and seasonal distribution of fish.

Fork length (mm), weight (g), sex and species (determined by peritoneal colour (Leim and Scott, 1966)) were recorded for each fish. Whole digestive tracts, individually identified, were preserved in 4% buffered formalin.

### Diet analysis

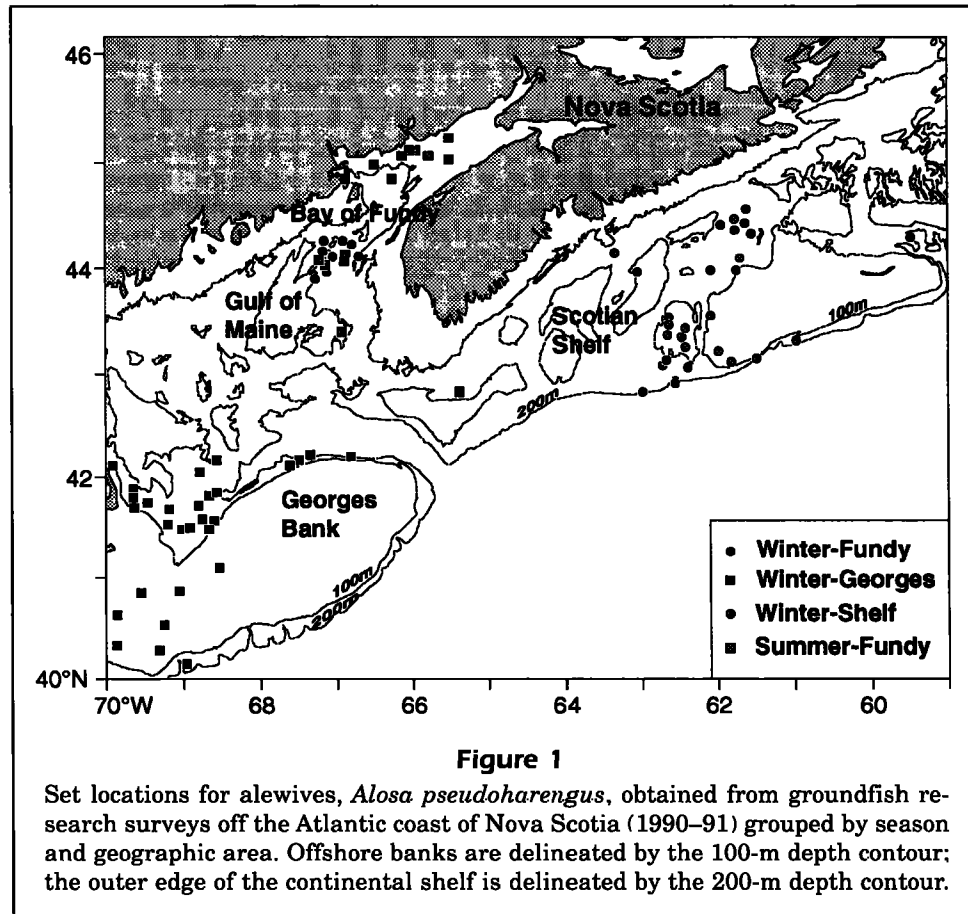
Stomachs were weighed ( $\pm 0.01$  g) and the contents ranked subjectively using a fullness code (0=empty, 1=12% full, 2=25% full, 3=50% full, 4=75% full, 5=100% full) and a digestion code (1=finely digested, nothing recognizable; 2=medium digestion, some recognizable parts; 3=some digested, some undigested material; 4=undigested whole animals). The stomach content weight was obtained by subtracting the weight of the empty stomach from the total stomach weight. Stomach content weight, as a percentage of fish body weight (%BW), was used as an index of fullness to evaluate feeding activity and estimate daily ration. Stomach contents were identified (to species where possible), enumerated, and the volume of each food type estimated by means of a points system (Swynnerton and Worthington, 1940; Stone and Daborn, 1987).

For diet analysis, prey taxa (Table 2) were grouped into nine categories based on taxonomy and ecology: 1) euphausiids (*Meganyctiphanes norvegica* and some *Thysanoessa* spp.); 2) hyperiid amphipods (*Parathemisto gaudichaudi*); 3) calanoid copepods (*Calanus* spp., *Centrophages* spp. and *Metridia* spp.); 4) polychaetes (*Nereis* spp. and unidentifiable species); 5) fish larvae (*Ammodytes dubius* and unidentifiable species); 6) mysids (*Neomysis americana*); 7)

**Table 1**

Stomach and fork length statistics, by season and geographic area, for alewives, *Alosa pseudoharengus*, obtained from groundfish research surveys conducted off Nova Scotia (1990–1991).

Season and area	Collection date		Number			Fork length (mm)	
	1990	1991	Sets	Stomachs	Stomachs with prey	Mean $\pm$ SD	Range
Winter-Fundy	2–10 Feb	—	9	112	58	201.9 $\pm$ 5.38	100–303
Winter-Georges	28 Feb–Mar 7	Feb 16–26	29	438	147	193.6 $\pm$ 1.83	118–305
Winter-Shelf	13–19 Mar	Mar 15–18	29	489	322	223.8 $\pm$ 2.82	95–302
Summer-Fundy	6–10 Jul	Jul 05–09	15	176	141	242.6 $\pm$ 2.48	142–302
Total			82	1,215	668	213.6 $\pm$ 1.86	95–305



chaetognaths; 8) crustacean larvae (furciliae of *Thysanoessa* spp. and some decapod larvae); and 9) pteropods. The percent frequency of occurrence (%FO), percent of total stomach content number (%N), and percent of total stomach content volume (%V) of prey categories were estimated for stomachs containing recognizable food (digestion code  $\geq 2$ ). The Index of Relative Importance ( $IRI = (\%N + \%V) \times \%FO$ ) was calculated for each prey category (Pinkas et al., 1971) and used for various diet comparisons. Diets were analyzed by season and geographic area (Winter-Fundy, Winter-Georges, Winter-Shelf, Summer-Fundy), as well as by depth range within season and area, to compare food items from shallow regions and offshore banks (<100 m), mid-depths (101–200 m) and the shelf edge or deep basins (>200 m). Diel differences in diet composition (day and night, based on time of gear deployment) were examined for the entire data set. Ontogenetic differences in diet within season/area were examined by grouping fish lengths into four size classes (<151, 151–200, 201–250 and >250 mm FL), which were assumed sufficient for detecting shifts in prey composition. Data from 1990 and 1991 were combined for all compari-

sons because the ranks of IRI values for all prey categories between years were highly correlated (Spearman rank correlation coefficient ( $r_s$ )=0.67;  $P < 0.05$ ;  $n=9$ ).

### Predator-prey size analysis

Total lengths ( $\pm 1$  mm, tip of rostrum to end of telson) of undigested, whole *M. norvegica* in the stomachs of 55 alewives (>200 mm FL, since most intact prey occurred only in larger fish) from Winter-Georges, Winter-Shelf, and Summer-Fundy cruises were compared with predator size. *Thysanoessa* spp. were not measured because of poor condition. Lengths of *M. norvegica* from Emerald Basin collected in June 1991, by Sameoto et al. (1993) using the Bedford Institute of Oceanography Net and Environmental Sensing System (BIONESS) were compared with euphausiid length frequencies from stomach contents to estimate the proportion of the available size range of *M. norvegica* consumed by alewives. The BIONESS is not considered to be size-selective for euphausiids (Sameoto et al., 1980).

### Diel feeding periodicity and daily ration estimate

Diel feeding periodicity and daily ration were examined separately for winter (Bay of Fundy, Scotian Shelf, and Georges Bank combined) and summer (Bay of Fundy) collections because of seasonal differences in photoperiod. Stomach fullness data from tows within each successive 3-hour (winter cruises) and 4-hour (summer cruises) interval were grouped and assigned to the midpoint of the time period. Small sample sizes precluded grouping of summer collections into 3-hour intervals.

Daily ration (DR) of alewives during winter and summer and by size class during winter (<151 mm, 151–200 mm, 201–250 mm, >250 mm) was estimated in terms of % body weight from the model of Elliott and Persson (1978):

$$C_t = \frac{(S_t - S_0 e^{-Rt})}{1 - e^{-Rt}} Rt;$$

where the consumption of food ( $C_t$ ) during the time interval  $t_0$  to  $t_t$  is calculated from the average amount of food in the stomach at time  $t_0$  ( $S_0$ ), the amount in the stomach at time  $t_t$  ( $S_t$ ) and the instantaneous evacuation rate  $R$ . The estimates of  $C_t$  calculated for each time interval are then summed to give the total daily ration (DR). Feeding is assumed constant within each time interval.  $R$  is assumed exponential and temperature dependent (Elliott, 1972), as

$$R = ae^{bT}.$$

The slope ( $b$ ) may be fairly constant for different prey types and fish species (mean=0.115), but the intercept ( $a$ ) changes with prey type and can be estimated from gastric evacuation experiments (Durbin et al., 1983). Gastric evacuation rate data are unavailable for anadromous alewives; therefore, an intercept ( $a=0.0406$ ) was obtained from Durbin et al. (1983) based on values for a variety of small invertebrates fed to several freshwater and marine fishes. High fat levels in the prey may retard evacuation (Durbin et al., 1983) but the principal food item in this study (*M. norvegica*) has a low lipid content (Ackman et al., 1970). Average bottom temperatures for winter (mean=7.16°C) and summer (mean=7.43°C) collections were used to estimate  $R$ .

### Statistical analysis

Differences in the rankings of IRI values for prey categories ( $n=8$ ) between three or more groups were tested for significance with the Kendall coefficient

of concordance ( $w$ ) (Siegel, 1956); for paired groups, the Spearman rank correlation coefficient ( $r_s$ ) was used (Fritz, 1974). Euphausiids, which consistently ranked highest in importance in all comparisons, were excluded from correlation analysis to reduce bias and emphasize correlations among remaining prey groups.

One-way ANOVA was used to examine feeding activity, represented by the index of fullness (arc-sine  $\sqrt{p}$  transformed) by season and geographic area, by depth range within season and geographic area and by diel sampling period (winter and summer collections) and to compare total lengths of euphausiid prey. Paired means, adjusted for unequal sample sizes, were compared with the Tukey-Kramer test (Sokal and Rohlf, 1981). The relation between predator fork length and mean prey length was examined by linear regression for alewives with three or more *M. norvegica* present in their stomachs.

### Results

Alewives examined for stomach contents measured 95 to 305 mm FL (mean=213.6 mm,  $n=1,215$ ); fish from summer cruises in the Bay of Fundy were larger on average than those from other collections (Table 1). Capture depths ranged from 36 to 269 m, although most (75%) specimens were obtained from regions 101 to 200 m deep.

Recognizable prey from over 20 different taxa occurred in 55% (668 of 1,215) of stomachs examined (Table 2). Over 95% of the total prey number, volume, and frequency of occurrence were crustaceans (Table 2). Euphausiids were the most prevalent (91% by volume); *Meganyctiphanes norvegica* were dominant by volume (61%) and furcilia larvae of *Thysanoessa* spp. were dominant numerically (32%). Other prey, including hyperiid amphipods, calanoid copepods, crustacean larvae, mysids, polychaetes, chaetognaths, pteropods, and fish larvae contributed little and varied temporally and spatially in relative importance.

### Diet composition by season and area

Euphausiids were the most important food of alewives during winter and summer for all areas (Fig. 2). During winter, alewives from the outer Bay of Fundy and Georges Bank fed almost exclusively on euphausiids (99% and 95% of total volume, respectively). On Georges Bank, small (%V≤3) proportions of calanoid copepods, hyperiid amphipods, and pteropods were also consumed. Prey diversity was greatest for alewives from the Scotian Shelf; euphausiids dominated by volume (82%) but were numeri-

Table 2

Prey items found in the stomachs of alewives, *Alosa pseudoharengus*, collected from groundfish research surveys off Nova Scotia, 1990–91. %FO = percent frequency of occurrence, %N = percent by number, %V = percent by volume.

Prey item	%FO	%N	%V	Prey item	%FO	%N	%V
Crustacea	97.6	95.0	97.3	Decapoda	0.5	0.1	<0.1
Euphausiacea	91.3	72.4	91.0	Zoea	0.2	<0.1	<0.1
<i>Meganyctiphanes norvegica</i>	37.7	29.4	60.9	Megalopa	0.3	0.1	<0.1
<i>Thysanoessa</i> spp	6.9	4.5	6.0	Cirripedia Cypris larvae	0.2	<0.1	<0.1
<i>Thysanoessa</i> spp furcillia	3.7	32.1	1.2	Insecta Hymenoptera	0.5	<0.1	<0.1
Unidentified Euphausiacea	40.1	6.3	23.0	Polychaeta	1.8	0.1	0.5
Amphipoda	15.9	4.7	4.8	<i>Nereis</i> spp	1.1	0.1	0.4
Hyperiidea	15.6	4.2	4.4	Unidentified Polychaeta	0.8	<0.1	0.1
<i>Parathemisto gaudichaudi</i>	9.9	3.1	2.9	Chaetognatha	1.1	3.6	<0.5
Unidentified Hyperiidea	5.7	1.0	1.5	Hydrozoa	0.3	—	<0.1
Gammaridea	0.3	0.5	0.4	Gastropoda Pteropoda ( <i>Limacina</i> )	5.1	0.8	0.3
Caprellidea	0.2	<0.1	<0.1	Teleost larvae	3.9	0.5	1.4
Copepoda	8.2	17.4	1.2	<i>Ammodytes dubius</i>	2.7	0.5	1.0
Calanoidea				Unidentified fish larvae	1.2	<0.1	0.4
<i>Centrophages</i> spp	3.1	1.3	0.2	Algae	1.2	—	0.2
<i>Calanus</i> spp	0.5	0.7	<0.1	Organic material	0.6	—	<0.1
<i>Metridia</i> spp	2.0	1.1	<0.1	Unidentified remains	6.6	—	0.8
Unidentified calanoids	6.9	14.3	0.9	Total stomachs with food	668		
Mysidacea				Total prey number	14,752		
<i>Neomysis americana</i>	0.2	0.4	0.2	Total prey volume (points)	25,232		
Cumacea	0.3	<0.1	<0.1				

cally less than in other areas. Hyperiid amphipods, (*Parathemisto gaudichaudi*), ranked second in importance (%V=10), followed by crustacean larvae (furcilliae), calanoid copepods, and fish larvae, (*Ammodytes dubius*). During summer in the Bay of Fundy, alewives fed heavily on euphausiids (%V=95) but also consumed chaetognaths, mysids, and polychaetes (second, third, and fourth in importance).

Rankings of IRI values (excluding euphausiids) for Winter-Georges, Winter-Shelf, and Summer-Fundy samples were not significantly correlated ( $w=0.22$ ,  $P=0.701$ ), indicating seasonal and geographic differences in the dietary importance of these lesser prey categories. Winter-Fundy samples contained too few prey categories to be analyzed.

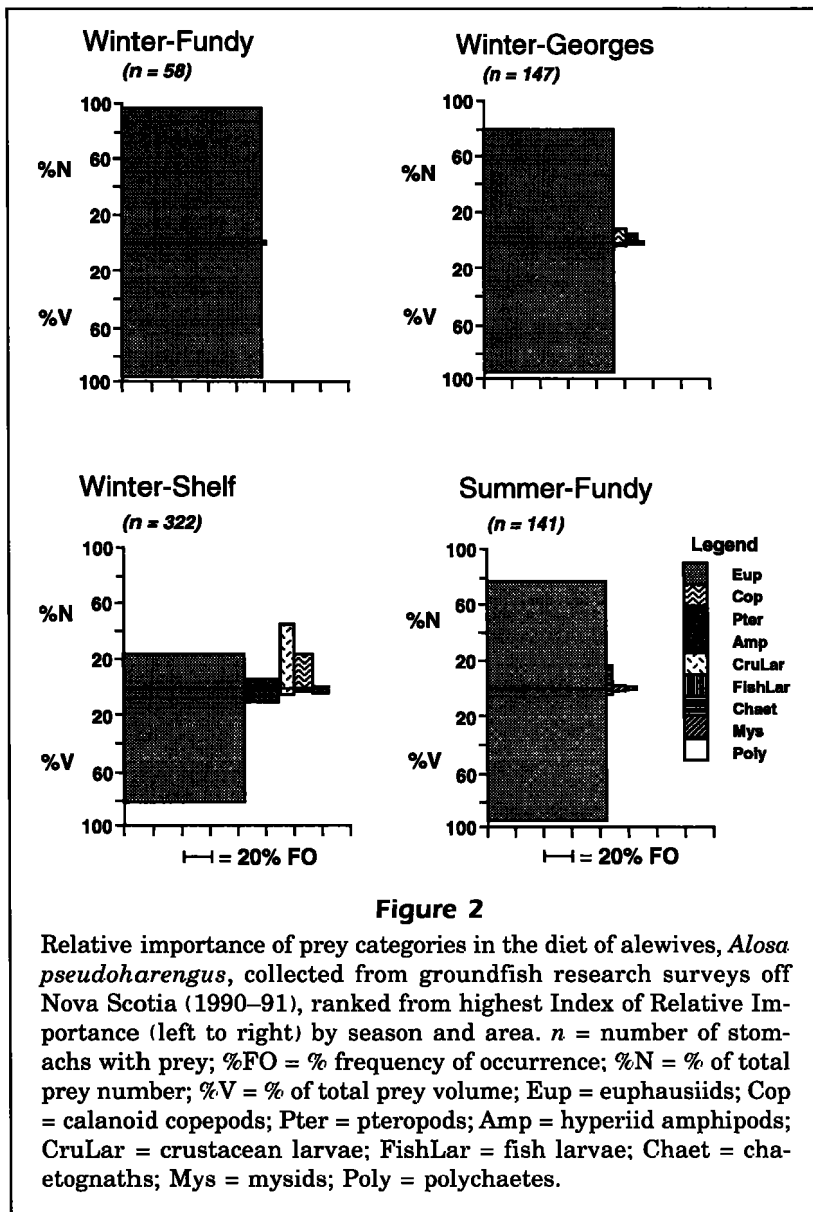
### Diet composition by depth range

For Winter-Shelf and Summer-Fundy collections, the proportion of euphausiids in the diet increased with increasing depth (Fig. 3). At bottom depths less than 101 m on the Scotian Shelf, euphausiids composed 64% of total volume and 22% of total number; at 101 to 200 m, %V = 83 and %N = 23 and at depths

greater than 200 m, %V = 96 and %N = 95. During summer in the Bay of Fundy, euphausiid consumption increased with depth such that at less than 101 m, %V = 82 and %N = 35; at 101 to 200 m, %V = 97 and %N = 97; while at depths greater than 200 m, both %V and %N = 100. Other prey categories generally decreased in number with increasing depth as did their relative proportion. For both Winter-Shelf and Summer-Fundy collections, prey diversity and abundance were greatest where bottom depths were less than 101 m.

Multiple correlations of IRI values for prey categories (excluding euphausiids) between the three bottom-depth interval groups were not significant ( $w=0.54$ ,  $P=0.12$ ) for Scotian Shelf collections and reflect the decreasing number of prey categories with increasing depth. For Summer-Fundy samples, the Spearman rank correlation of IRI values for the two shallower depth-intervals was not significant ( $r_s=-0.35$ ,  $P>0.05$ ) and euphausiids were the only prey at depths greater than 200 m.

Depth-related differences did not occur in the euphausiid-dominated diet of alewives from the Winter-Fundy and Winter-Georges collections at



bottom depths exceeding 101 m (no fish were obtained at bottom depths less than 101 m). IRI rankings of prey categories between depth groups for Georges Bank collections were highly correlated ( $r_s=0.89$ ,  $P<0.01$ ). Too few prey categories were present for analysis of Winter-Fundy collections. In both winter and summer, most euphausiids consumed at depths less than 101 m were *Thysanoessa* spp. which are smaller than *M. norvegica* and prefer shallower regions (Table 3).

#### Diel variation in the diet

Although euphausiids occurred in over 85% of alewife stomachs from day and night collections, higher

numbers and volumes were ingested during the day (%N=74, %V=92) than at night (%N=16, %V=85) (Fig. 4). IRI values for day and night collections were not significantly correlated ( $r_s=0.26$ ,  $P>0.05$ ) reflecting the greater consumption of hyperiid amphipods during the day and copepods, crustacean larvae and fish larvae at night.

#### Diet composition by size class

Diet composition was relatively homogeneous among alewife size groups (<151 mm, 151–200 mm, 201–250 mm, >250 mm) with euphausiids composing most of the total food volume (Fig. 5). Multiple correlations of IRI values for prey categories (excluding euphausiids) by fish length group were significant for both the Scotian Shelf ( $w=0.58$ ,  $P=0.024$ ) and Georges Bank ( $w=0.65$ ,  $P=0.011$ ). For Summer-Fundy collections, diets of the two largest size groups were nearly identical; IRI values were not significantly correlated ( $r_s=0.38$ ,  $P>0.05$ ) due to slight differences in the rankings of minor prey categories (i.e., amphipods, mysids, polychaetes, chaetognaths).

#### Prey size composition

Alewives ingested similar sizes of *M. norvegica* during winter (Georges Bank, Scotian Shelf) and summer (Bay of Fundy) (Fig. 6). Modal peaks in euphausiid size appeared at 25–27

mm and 30 mm on the Scotian Shelf and at 30–35 mm for Georges Bank and the Bay of Fundy. In comparison, *M. norvegica* from Emerald Basin BIONESS collections in June 1991 were bimodally distributed at 25–27 mm and 34 mm. Euphausiids larger than 29 mm were proportionately less frequent than in stomach contents.

Mean lengths of *M. norvegica* consumed by alewives varied by season/area group ( $F_{2,701}=65.5$ ,  $P<0.001$ ), although differences between means were small (Winter-Georges: mean=32.1±3.13; Winter-Shelf: mean=28.7±3.72; Summer-Fundy: mean=31.2±3.64). The average size of euphausiids consumed did not differ ( $F_{1,50}=3.31$ ,  $P=0.075$ ) with alewife size (range: 225–300 mm FL).

## Feeding activity

Feeding activity, as indicated by mean stomach fullness index values, varied by season/geographic area ( $F_{3,1210}=46.20$ ,  $P<0.001$ ). Mean stomach fullness was highest for Summer-Fundy and Winter-Shelf collections and lowest for Winter-Fundy and Winter-Georges collections (Table 4). The proportion of feeding fish was highest during summer in the Bay of Fundy (80.6%) and lowest during winter on Georges Bank (33.6%). Stomach fullness was significantly higher at bottom depths greater than 200 m for all but the Winter-Shelf collections, where mean fullness did not differ among depth groups (Table 4). Similarly, the proportion of feeding fish was highest in areas exceeding 200 m deep for all collections.

Alewife feeding activity varied throughout the diel period during winter ( $F_{7,1031}=24.97$ ,  $P<0.001$ ) and summer ( $F_{5,196}=7.98$ ,  $P<0.001$ ) with maximum fullness in both seasons occurring near mid-day (Fig. 7). In winter, feeding activity was extremely variable: mean fullness was high during early morning (0001–0430 hours), declined until dawn (0730), increased sharply until early afternoon (1330), declined again in late afternoon (1630) and then increased after sunset before falling off again prior to midnight. During summer, diel feeding activity was much more constant, although sample sizes were smaller and stomach fullness more variable. Feeding activity increased gradually after sunrise, peaked by mid-morning (1000), then declined throughout the afternoon and evening until just prior to midnight (2200). Although alewives fed actively at night during winter, peak feeding generally occurred during the day in winter and summer.

## Daily ration

Daily consumption of alewives in the field was about 1.22% BW at 7.16°C during winter and 1.88% BW

at 7.43°C during summer (Table 5). The winter daily ration of alewives generally decreased from 1.95% BW for fish less than 151 mm FL to 1.13% BW at 151–200 mm FL, 1.19% BW at 201–200 mm FL and 1.00% BW at larger than 250 mm FL.

## Discussion

Our study clearly indicates that alewives off Nova Scotia feed primarily on euphausiids, particularly *Meganyctiphanes norvegica*; much smaller contributions are made by other prey. Alewives from the

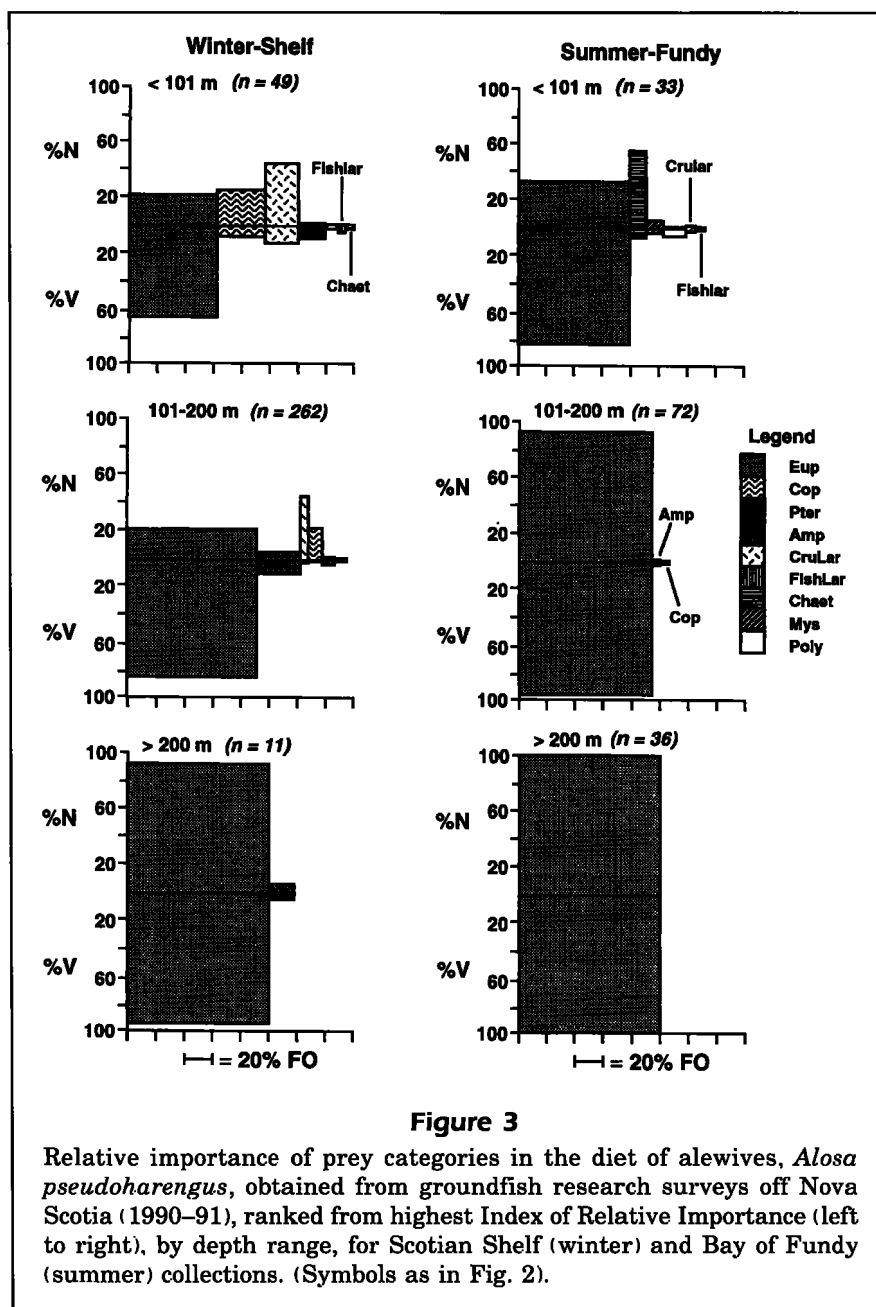


Figure 3

Relative importance of prey categories in the diet of alewives, *Alosa pseudoharengus*, obtained from groundfish research surveys off Nova Scotia (1990–91), ranked from highest Index of Relative Importance (left to right), by depth range, for Scotian Shelf (winter) and Bay of Fundy (summer) collections. (Symbols as in Fig. 2).

Table 3

Mean number of *Meganyctiphanes norvegica* and *Thysanoessa* spp. in the stomachs of alewives, *Alosa pseudoharengus*, by depth interval within season and geographic area from groundfish research surveys off Nova Scotia (1990–91).  $n$  = number of stomachs with prey.

Season and area	Depth (m)	<i>M. norvegica</i>				<i>Thysanoessa</i> spp.			
		Mean	±	SD	$n$	Mean	±	SD	$n$
Winter–Fundy	101–200	11.3	±	7.36	3	5.4	±	0.81	5
	>200	10.2	±	2.20	9	2.5	±	1.50	2
Winter–Georges	101–200	5.9	±	0.81	26	11.8	±	6.55	6
	>200	20.3	±	1.68	28	—	—	—	—
Winter–Shelf	<101	—	—	—	—	32.0	±	14.63	10
	101–200	14.7	±	1.41	89	9.6	±	3.79	20
	>200	5.8	±	3.47	4	—	—	—	—
Summer–Fundy	<101	18.9	±	3.47	14	12.0	±	2.00	2
	101–200	21.9	±	2.67	48	—	—	—	—
	>200	27.5	±	2.39	31	23.0	—	—	1

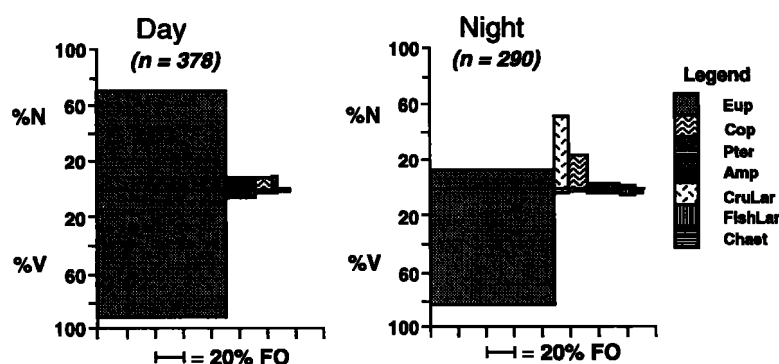


Figure 4

Relative importance of prey categories in the diet of alewives, *Alosa pseudoharengus*, obtained from groundfish research surveys off Nova Scotia (1990–91), ranked from highest Index of Relative Importance (left to right) for day and night collections (Symbols as in Fig. 2).

Atlantic seaboard of the United States consumed relatively fewer euphausiids (37–56% by weight) (Edwards and Bowman, 1979; Vinogradov, 1984) than off Nova Scotia (82–99% by volume).

Euphausiids represent a large component of the marine zooplankton community and are abundant in the Bay of Fundy (Kulka et al., 1982; Locke and Corey, 1988), Gulf of Maine (Bigelow, 1926), the deep basins of the Scotian Shelf (Herman et al., 1991) and the outer shelf and shelf slope (Sameoto, 1982). Given their two-year life cycle (Hollingshead and Corey, 1974; Berkes, 1976), the availability and relative abundance of euphausiids is more seasonally

stable than for other prey species (i.e., chaetognaths, hyperiid amphipods, calanoid copepods, mysids), most of which undergo fluctuations in abundance progressing from a spring low to a summer high before declining in fall and winter (Evans, 1968; Sherman and Schaner, 1968; Corey, 1988; McLaren et al., 1989).

Small seasonal differences in diet composition reflect the opportunistic foraging behaviour of alewives and the availability of food types from offshore regions during winter as compared with the Bay of Fundy in summer. During winter, the diet diversity of alewives was greatest on the Scotian Shelf probably because the late winter (mid-March) sampling period coincides with the hatching and occurrence of the larval forms of *Thysanoessa* spp. (Berkes, 1976) and *Ammodytes dubius* (Scott, 1972), both of which occurred only in the diet of alewives from the Scotian Shelf. In the Bay of Fundy, alewife consumption of chaetognaths and mysids in the summer reflects their increased abundance and availability (Sherman and Schaner, 1968; Corey, 1988).

The increased proportion of euphausiids in the diet of alewives from the Scotian Shelf (winter) and the Bay of Fundy (summer) coincides with an increased relative abundance of euphausiids with increasing depth. In the Scotian Shelf Basins, *M. norvegica* occur between 170 m and the bottom with highest concentrations generally below 200 m (Sameoto et al., 1993). In the Bay of Fundy, *M. norvegica* is most abundant where bottom depths are between 165 and 200 m, while *Thysanoessa inermis* occur between 95 and 155 m (Kulka et al., 1982). The greater proportion and number of other prey categories at depths less than 101 m on the Scotian Shelf and in the Bay of Fundy likely result from decreased euphausiid abundance (thereby increasing the relative contribution of other prey) rather than an absolute increase in the abundance of other zooplankters. Depth-related variation in



euphausiid species composition in the diet of alewives from all regions matches differences in the bottom depth preferences of *M. norvegica* (>150 m) and *Thysanoessa* spp. (100–150 m) (Berkes, 1976; Kulka et al., 1982; Sameoto et al., 1993).

Diel differences in the diet of alewives may reflect the influence of varying light intensity on prey availability and on their relative success in locating and capturing prey. Consumption of microzooplankters (crustacean larvae, calanoid copepods) was greater at night perhaps because of increased filter-feeding activity (Janssen, 1978b). Conversely, ingestion of macrozooplankters (euphausiids, hyperiid amphipods) may be highest during the day because visual cues favour a particulate-feeding mode.

Large size, darkly pigmented eyes, and a habit of forming large concentrations (Mauchline and Fisher, 1969) may make *M. norvegica* easily detectable by alewives during daylight whereas at night, photophores along the abdomen of *M. norvegica* may assist detection. Most euphausiid species migrate vertically over the diel period, rising from deep water (150–200 m) towards the surface at dusk, remaining near surface throughout the night, and then migrating to the depths at dawn (Mauchline, 1984). Alewives also have a diel pattern of vertical migration in the marine environment (Neves, 1981; Stone and Jessop, 1992) and may encounter sufficient light higher in the water column at night to particulate feed on euphausiids.

Ontogenetic differences in diet composition were not apparent; euphausiids dominated the diet of alewives ranging in length from 95 to 305 mm. Alewives switch from feeding primarily on microzooplankton to macrozooplankton at some point during their marine development and like other similarly sized clupeids, concentrate their feeding at intermediate trophic levels (James, 1988).

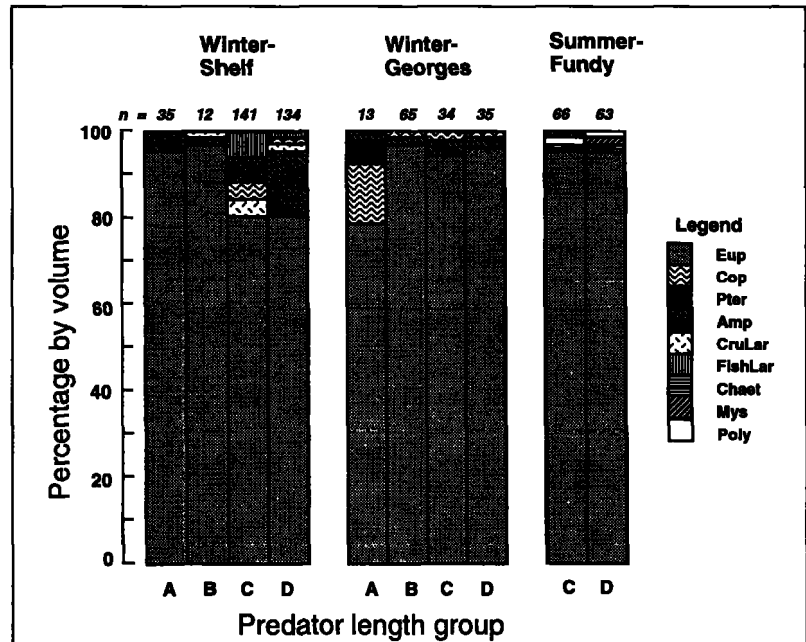


Figure 5

Percentage of total volume of prey categories in the diet of alewives, *Alosa pseudoharengus*, for different size classes (mm FL) obtained from groundfish research surveys off Nova Scotia (1990–91). Euphausiids were the only prey category in Winter-Fundy cruises. A: <151 mm; B: 151–200 mm; C: 201–250 mm; D: >250 mm; Eup = euphausiids; Cop = calanoid copepods; Pter = pteropods; Amp = hyperiid amphipods; CruLar = crustacean larvae; FishLar = fish larvae; Chaet = chaetognaths; Mys = mysids; Poly = polychaetes; n = number of stomachs with food.

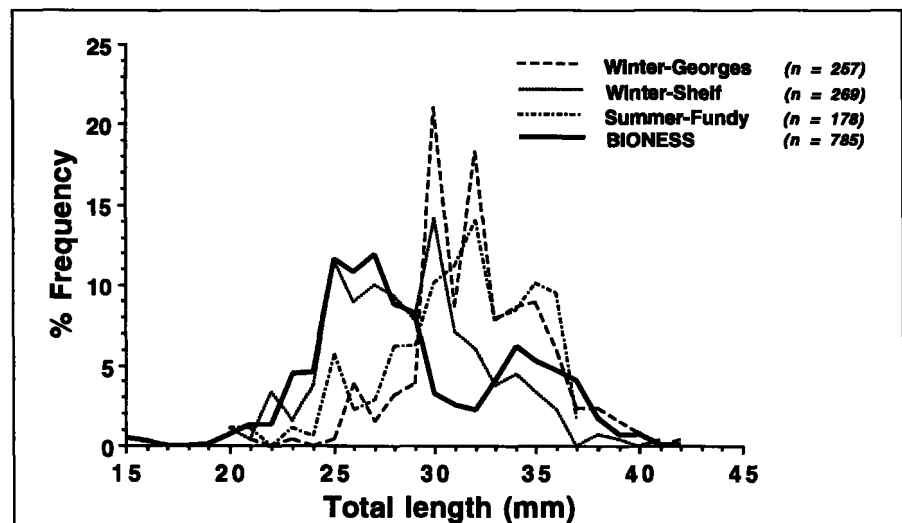


Figure 6

Size frequency distributions of *M. norvegica* consumed by alewives, *Alosa pseudoharengus*, obtained from winter (Georges Bank, Scotian Shelf) and summer (Bay of Fundy) groundfish surveys off Nova Scotia (1990–91) and from BIONESS samples in Emerald Basin (Spring, 1991). n = sample size.

Table 4

Mean stomach fullness index (arcsine  $\sqrt{p}$  transformed) by season and geographic area and by depth interval for alewives, *Alosa pseudoharengus*, obtained from groundfish research surveys off Nova Scotia (1990–91). Mean fullness index values lacking a letter in common are significantly different (Tukey HSD,  $P < 0.05$ ).  $n$  = number of stomachs examined (including empty stomachs).

Season and area	Depth (m)	$n$	% with food	Fullness index (%BW)		
				Mean	$\pm$ SD	Maximum
Winter–Fundy	all	112	51.8	2.3z	$\pm$ 0.25	9.9
Winter–Georges	all	438	33.6	2.1z	$\pm$ 0.13	9.9
Winter–Shelf	all	489	65.0	3.8y	$\pm$ 0.10	10.0
Summer–Fundy	all	175	80.6	3.9y	$\pm$ 0.21	10.0
Winter–Fundy	101–200	60	28.3	1.5z	$\pm$ 0.29	9.4
	>200	52	78.8	3.7y	$\pm$ 0.32	9.9
Winter–Georges	<101	7	28.6	2.1z	$\pm$ 0.87	5.9
	101–200	376	28.7	1.7z	$\pm$ 0.12	9.9
	>200	55	67.3	4.6y	$\pm$ 0.46	9.9
Winter–Shelf	<101	92	55.3	3.4z	$\pm$ 0.16	7.4
	101–200	385	68.1	3.9z	$\pm$ 0.12	10.0
	>200	12	91.7	3.4z	$\pm$ 0.46	8.0
Summer–Fundy	<101	48	68.8	3.5z	$\pm$ 0.33	8.8
	101–200	87	82.8	3.6z	$\pm$ 0.30	10.0
	>200	40	90.1	5.0y	$\pm$ 0.51	9.8

Gilmurray (1980) found mainly microplanktonic prey (e.g., calanoid copepods, cypris larvae, insects) in the diet of alewives less than 80 mm FL obtained from tidal creeks in the upper Bay of Fundy. The shift towards consumption of macrozooplankton likely occurs at fish sizes smaller than those examined in the present study (i.e., <95 mm FL).

Diel feeding activity during winter and summer, as indicated by the mean fullness index, reached a maximum near mid-day and is typical of size-selective predators which rely on visual cues (Eggers, 1977). Summer resident subadult alewives in Minas Basin display a similar feeding pattern, although peak feeding occurred later in the afternoon (1500 hours), coincident with the time of high tide when turbidity was lowest and prey visibility highest (Stone, 1985). Summer feeding activity by juvenile anadromous alewives in freshwater also peaks during the day but ceases or declines overnight (Jessop, 1990). Nocturnal feeding by alewives was more apparent during winter than summer; the significance of this seasonal difference in feeding activity is unclear. Alewives can and do feed efficiently at night using both particulate (Janssen and Brandt, 1978)

and filter-feeding (Janssen, 1978b) modes.

Alewives greater than 200 mm FL generally consumed the largest *Meganyctiphanes* available. Length-frequency distributions of *M. norvegica*, which has a life span of about two years, are typically bimodal (Hollingshead and Corey, 1974; Berkes, 1976). Alewives selectively favor larger prey (Brooks and Dodson, 1965; Brooks, 1968; Wells, 1970) and likely use a particulate feeding strategy in doing so. Slight seasonal and geographic differences in the average size of *M. norvegica* ingested likely reflect size differences in euphausiid populations rather than selection by the predator.

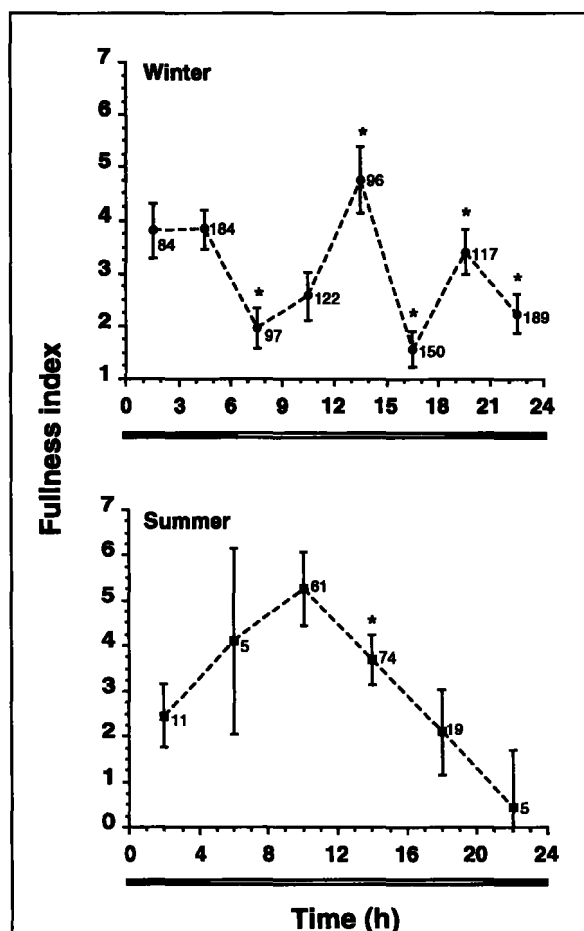
Daily ration calculations were based on the model of Elliott and Persson (1978) which was originally intended for field samples collected within a given area from the same population over time. Our stomach fullness data for alewives from the Bay of Fundy, Georges

Bank, and the Scotian Shelf covered a wide area geographically and may involve more than one population. The broad temporal and spatial coverage reduces the effect of day-to-day and regional variations in diet which would arise from more restricted sampling. Calculated daily ration levels for alewives off Nova Scotia were similar to those reported for other teleosts (Fänge and Grove, 1979). Lower estimates were obtained during winter (1.22% BW at 7.16°C) than for summer (1.88% BW at 7.43°C) since temperature is related to metabolic requirements and to the evacuation rate of stomach contents (Durbin et al., 1983). Both estimates are well above maintenance ration levels for temperatures in the 7–8°C range and are sufficient for positive growth (Brett and Groves, 1979). Alewife daily ration declined with increasing fish size; small fish, including marine species such as North Sea cod, *Gadus morhua* (Daan, 1973), winter flounder, *Pseudopleuronectes americanus* (Huebner and Langton, 1982) and silver hake, *Merluccius bilinearis* (Durbin et al., 1983), generally consume proportionally more food per unit weight than large fish (Windell, 1978). Overall, our estimates of daily

Table 5

Mean amount of food (%BW) in the stomachs of alewives, *Alosa pseudoharengus*, obtained from groundfish surveys off Nova Scotia (1990–91), with estimates of food consumption ( $C_t$ ) and daily ration ( $DR = \Sigma C_t$ ), by season and size class.  $n$  = number of stomachs examined (including empty stomachs. For winter collections,  $R = 0.0925$ , temperature =  $7.16^\circ\text{C}$ ; for summer collections,  $R = 0.0954$ , temperature =  $7.43^\circ\text{C}$ .

Season (size class)	Time period (hr)	$n$	Stomach contents (%BW)		$C_t$ (%BW)	DR (%BW)
			Mean	$\pm$ SD		
Winter (all)	2400–0300	84	0.75	$\pm$ 0.100		1.216
	0300–0600	184	0.65	$\pm$ 0.053	0.098	
	0600–0900	97	0.23	$\pm$ 0.038	–0.308	
	0900–1200	122	0.52	$\pm$ 0.079	0.401	
	1200–1500	96	1.09	$\pm$ 0.104	0.792	
	1500–1800	150	0.20	$\pm$ 0.032	–0.709	
	1800–2100	177	0.52	$\pm$ 0.043	0.421	
	2100–2400	189	0.42	$\pm$ 0.053	0.033 0.488	
Summer (all)	2400–0400	11	0.22	$\pm$ 0.041		1.880
	0400–0800	5	0.58	$\pm$ 0.198	0.515	
	0800–1200	61	2.32	$\pm$ 0.161	2.316	
	1200–1600	74	1.32	$\pm$ 0.190	–0.320	
	1600–2000	19	0.48	$\pm$ 0.249	–0.508	
	2000–2400	5	0.03	$\pm$ 0.031	–0.357 0.234	
Winter (<151 mm FL)	2400–0400	29	0.95	$\pm$ 0.233		1.949
	0400–0800	31	1.13	$\pm$ 0.146	0.563	
	0800–1200	4	0.90	$\pm$ 0.382	0.143	
	1200–1600	3	1.32	$\pm$ 0.439	0.842	
	1600–2000	13	0.42	$\pm$ 0.110	–0.593	
	2000–2400	87	0.55	$\pm$ 0.103	0.311	
Winter (151–200 mm FL)	2400–0300	22	1.10	$\pm$ 0.199		1.126
	0300–0600	48	0.61	$\pm$ 0.095	–0.253	
	0600–0900	26	0.12	$\pm$ 0.048	–0.396	
	0900–1200	29	0.22	$\pm$ 0.063	0.151	
	1200–1500	9	0.84	$\pm$ 0.532	0.765	
	1500–1800	69	0.14	$\pm$ 0.039	–0.565	
	1800–2100	26	0.74	$\pm$ 0.153	0.719	
	2100–2400	25	0.16	$\pm$ 0.053	–0.457	
Winter (201–250 mm FL)	2400–0300	30	0.52	$\pm$ 0.094		1.189
	0300–0600	60	0.62	$\pm$ 0.093	0.256	
	0600–0900	23	0.27	$\pm$ 0.062	–0.222	
	0900–1200	51	0.53	$\pm$ 0.123	0.372	
	1200–1500	27	0.93	$\pm$ 0.192	0.600	
	1500–1800	56	0.31	$\pm$ 0.065	–0.453	
	1800–2100	42	0.61	$\pm$ 0.075	0.434	
	2100–2400	36	0.50	$\pm$ 0.093	0.046 0.156	
Winter (>250 mm FL)	2400–0300	14	0.24	$\pm$ 0.052		1.000
	0300–0600	34	0.32	$\pm$ 0.042	0.161	
	0600–0900	47	0.27	$\pm$ 0.067	0.029	
	0900–1200	39	0.68	$\pm$ 0.173	0.545	
	1200–1500	57	1.19	$\pm$ 0.124	0.772	
	1500–1800	22	0.11	$\pm$ 0.032	–0.902	
	1800–2100	39	0.31	$\pm$ 0.076	0.257	
	2100–2400	11	0.50	$\pm$ 0.141	0.302	



**Figure 7**

Diel feeding chronology of alewives, *Alosa pseudoharengus*, from winter and summer groundfish research surveys off Nova Scotia (1990-91), as determined from changes in fullness index values. Data are means (arc-sine  $\sqrt{p}$  transformed with 95% confidence intervals) placed at the midpoint of each 3-hour (winter) and 4-hour (summer) interval. Asterisk denotes mean significantly different ( $P < 0.05$ ) from that of previous time interval. Sample size is adjacent to each symbol. Open and solid portions of horizontal bars represent light and dark hours during winter and summer.

ration may be on the low side because of possible weight loss in *M. norvegica* due to the effects of formalin preservation (Steedman, 1976). However, weight loss in euphausiids preserved for up to one year would likely be less than 10% because of their large size and low lipid content (Sameoto, 1993<sup>1</sup>).

The higher mean stomach fullness indices during summer in the Bay of Fundy and winter on the Scotian Shelf indicate that these regions are seasonally important foraging areas for alewives. Off Nova Scotia, alewives fed most actively (judged by the proportion of feeding fish and their stomach fullness) where oceanic conditions, particularly depth ( $>200$  m) and temperature, were suitable for *M. norvegica* (Kulka et al., 1982; Sameoto et al., 1993). Alewives prefer bottom temperatures of 7-11°C offshore at mid-depths in spring (101-183 m), in shallower nearshore waters in summer (46-82 m) and in deeper offshore waters in fall (119-192 m) (Stone and Jessop, 1992). During winter, *Meganyctiphanes* seeks deeper, warmer water rather than the cold upper layers (Bigelow, 1926; Hollingshead and Corey, 1974). While the seasonal pattern of movement by alewives (inshore and northward during spring and offshore and southward during fall) is partially linked with spawning migrations, it is apparent that their marine distribution is also influenced by the distribution, availability, and abundance of their main prey, *M. norvegica*.

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## Literature cited

- Ackman, R. G., C. A. Eaton, J. C. Sipos, S. N. Hooper, and J. D. Castell.  
1970. Lipids and fatty acids of two species of North Atlantic krill (*Meganyctiphanes norvegica* and *Thysanoessa inermis*) and their role in the aquatic food web. *J. Fish. Res. Board Can.* 27:513-533.
- Berkes, F.  
1976. Ecology of euphausiids in the Gulf of St. Lawrence. *J. Fish. Res. Board Can.* 33:1894-1905.
- Bigelow, H. G.  
1926. Plankton of the offshore waters of the Gulf of Maine. *Bull. U.S. Bur. Fish.* 40:1-509.
- Bigelow, H. B., and W. C. Schroeder.  
1953. Fishes of the Gulf of Maine. *Bull. U.S. Fish Wildl. Serv.* 74, 577 p.
- Bowman, R. E.  
1986. Effect of regurgitation on stomach content data of marine fishes. *Env. Biol. Fish.* 16:171-181.

<sup>1</sup> D. Sameoto, Bedford Institute of Oceanography, Dartmouth, Nova Scotia B2Y 4A2, pers. commun. July 1993.

**Brett, J. R., and T. D. D. Groves.**

1979. Physiological energetics. In W. S. Hoar, D. J. Randall, and J. R. Brett (eds.), *Fish physiology*, Vol. 8, p. 280-344. Academic Press, New York.

**Brooks, J. L.**

1968. The effects of prey-size selection by lake planktivores. *Syst. Zool.* 17:272-291.

**Brooks, J. L., and S. I. Dodson.**

1965. The effect of a marine planktivore on lake plankton illustrates theory of size, competition and predation. *Science* 150:28-35.

**Corey, S.**

1988. Quantitative distributional patterns and aspects of the biology of the Mysidacea (Crustacea: Peracarida) in the zooplankton of the Bay of Fundy region. *Can. J. Zool.* 66:1545-1552.

**Daan, N.**

1973. A quantitative analysis of the food intake of North Sea cod, *Gadus morhua*. *Neth. J. Sea Res.* 6:479-517.

**Durbin, A. G.**

1979. Food selection by plankton feeding fishes. In H. Clepper (ed.), *Predator-prey systems in fisheries management*, p. 203-218. Sport Fishing Inst., Washington D.C.

**Durbin, E. G., A. G. Durbin, R. W. Langton, and R. E. Bowman.**

1983. Stomach contents of silver hake, *Merluccius bilinearis*, and Atlantic cod, *Gadus morhua*, and estimation of their daily rations. *Fish. Bull.* 81:437-454.

**Edwards, R. L., and R. E. Bowman.**

1979. Food consumed by continental shelf fishes. 87-409 In H. Clepper (ed.), *Predator-prey systems in fisheries management*, p. 387-409. Sport Fishing Inst., Washington D.C.

**Eggers, D. M.**

1977. Factors in interpreting data obtained by diel sampling of fish stomachs. *J. Fish. Res. Board Can.* 34:290-294.

**Elliott, J. M.**

1972. Rates of gastric evacuation in brown trout, *Salmo trutta* L. *Freshwater Biol.* 2:1-18.

**Elliott, J. M., and L. Persson.**

1978. The estimation of daily rates of food consumption for fish. *J. Anim. Ecol.* 47:977-991.

**Evans, F.**

1968. Development and reproduction of *Parathemisto gracilipes* (Norman) (Amphipoda, Hyperiidea) in the North Sea. *Crustaceana* 15:101-109.

**Fänge, R., and D. Grove.**

1979. Digestion. In W. S. Hoar, D. J. Randall, and J. R. Brett (eds.), *Fish physiology*, Vol. 8, p. 162-241. Academic Press, New York.

**Fritz, E. S.**

1974. Total diet comparison in fishes by Spearman rank correlation coefficients. *Copeia* 1974: 210-214.

**Gilmurray, M. C.**

1980. Occurrence and feeding habits of some juvenile fish in the southern bight of Minas Basin, Nova Scotia, 1979. Master's thesis, Acadia Univ., Wolfville, Nova Scotia, 100 p.

**Gregory, R. S., G. S. Brown, and G. R. Daborn.**

1983. Food habits of young anadromous alewives (*Alosa pseudoharengus*) in Lake Ainslie, Nova Scotia. *Can. Field Nat.* 97:423-426.

**Herman, A. W., D. D. Sameoto, C. Shunnian, W. R. Mitchell, B. Petrie, and N. Cochrane.**

1991. Sources of zooplankton on the Nova Scotia Shelf and their aggregations within deep shelf basins. *Cont. Shelf Res.* 11:211-238.

**Holland, B. J., and G. F. Yelverton.**

1973. Distribution and biological studies of anadromous fishes offshore North Carolina. N.C. Dep. Nat. Res. Spec. Sci. Rep. No. 24, 32 p.

**Hollingshead, K. W., and S. Corey.**

1974. Aspects of the life history of *Meganyctiphanes norvegica* (M. Sars), Crustacea (Euphausiacea), in Passamaquoddy Bay. *Can. J. Zool.* 52:495-505.

**Huebner, J. D., and R. W. Langton.**

1982. Rate of gastric evacuation for winter flounder, *Pseudopleuronectes americanus*. *Can. J. Fish. Aquat. Sci.* 39:356-360.

**James, A. G.**

1988. Are clupeid macrophagists herbivorous or omnivorous? A review of the diets of some commercially important clupeids. *S. Afr. J. Mar. Sci.* 7:161-177.

**Janssen, J.**

1976. Feeding modes and prey size selection in the alewife (*Alosa pseudoharengus*). *J. Fish. Res. Board Can.* 33:1972-1975.

- 1978a. Feeding-behaviour repertoire of the alewife, *Alosa pseudoharengus*, and the ciscoes, *Coregonus hoyi* and *C. artedii*. *J. Fish. Res. Board Can.* 35:249-253.

- 1978b. Will alewives (*Alosa pseudoharengus*) feed in the dark? *Env. Biol. Fish.* 3:239-240.

**Janssen, J., and S. B. Brandt.**

1978. Feeding ecology and vertical migration of adult alewives (*Alosa pseudoharengus*) in Lake Michigan. *Can. J. Fish. Aquat. Sci.* 37:177-184.

**Jessop, B. M.**

1990. Diel variation in density, length composition, and feeding activity of juvenile alewife, *Alosa pseudoharengus* Wilson, and blueback herring, *A. aestivalis* Mitchell, at near-surface depths in a hydroelectric dam impoundment. *J. Fish Biol.* 37:813-822.

**Kulka, D. W., S. Corey, and T. D. Isles.**

1982. Community structure and biomass of euphausiids in the Bay of Fundy. *Can. J. Fish. Aquat. Sci.* 39:326-334.

**Leim, A. H., and W. B. Scott.**

1966. Fishes of the Atlantic coast of Canada. *Fish. Res. Board Can. Bull.* 155, 485 p.

- Locke, A., and S. Corey.**  
1988. Taxonomic composition and distribution of Euphausiacea and Decapoda (Crustacea) in the neuston of the Bay of Fundy, Canada. *J. Plankton Res.* 10:185-198.
- Mauchline, J.**  
1984. Euphausiid, stomatopod and leptostracan crustaceans. E. J. Brill and W. Backhuys, London, 91 p.
- Mauchline, J., and L. R. Fisher.**  
1969. The biology of euphausiids. In F. S. Russel and M. Yonge (eds.), *Advances in marine biology*, Volume 7. Academic Press, London, 454 p.
- McLaren, I. A., M. J. Tremblay, C. J. Corkett, and J. C. Roff.**  
1989. Copepod production on the Scotian Shelf based on life-history analyses and laboratory rearings. *Can. J. Fish. Aquat. Sci.* 46:560-583.
- Neves, R. J.**  
1981. Offshore distribution of alewife, *Alosa pseudoharengus* and blueback herring, *A. aestivalis*, along the Atlantic coast. *Fish. Bull.* 79:473-485.
- Pinkas, L., M. S. Oliphant, and I. L. K. Iverson.**  
1971. Food habits of albacore, bluefin tuna and bonito in California waters. *Calif. Fish and Game Fish. Bull.* 152:1-105.
- Sameoto, D. D.**  
1982. Zooplankton and micronekton abundance in acoustic scattering layers on the Nova Scotian slope. *Can. J. Fish. Aquat. Sci.* 39:760-777.
- Sameoto, D. D., L. O. Jaroszynski, and W. B. Fraser.**  
1980. BIONESS, a new design in multiple net zooplankton samplers. *Can. J. Fish. Aquat. Sci.* 37:722-724.
- Sameoto, D., N. Cochrane, and A. Herman.**  
1993. Convergence of acoustic, optical, and net-catch estimates of euphausiid abundance: use of artificial light to reduce net-avoidance. *Can. J. Fish. Aquat. Sci.* 50:334-346.
- Scott, J. S.**  
1972. Eggs and larvae of northern sand lance (*Ammodytes dubius*) from the Scotian Shelf. *J. Fish. Res. Board Can.* 29:1667-1671.
- Sherman, K., and E. G. Schaner.**  
1968. Observations on the distribution and breeding of *Sagitta elegans* (Chaetognatha) in coastal waters of the Gulf of Maine. *Limnol. Oceanogr.* 13:618-625.
- Siegel, S.**  
1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill Book Co., Toronto, 312 p.
- Sokal, R. R., and F. J. Rohlf.**  
1981. *Biometry*, 2nd ed. H. Freeman, San Francisco, 859 p.
- Steedman, H. F.**  
1976. General and applied data on formaldehyde fixation and preservation of marine zooplankton. In H. F. Steedman (ed.), *Zooplankton fixation and preservation*, p. 103-154. Unesco Press, Paris, 350 p.
- Stone, H. H.**  
1985. Composition, morphometric characteristics and feeding ecology of alewives (*Alosa pseudoharengus*) and blueback herring (*A. aestivalis*) (Pisces: Clupeidae) in Minas Basin. Master's thesis, Acadia Univ., Wolfville Nova Scotia, 191 p.
- Stone, H. H., and G. R. Daborn.**  
1987. Diet of alewives, *Alosa pseudoharengus* and blueback herring, *A. aestivalis* (Pisces: Clupeidae) in Minas Basin, Nova Scotia, a turbid macrotidal estuary. *Env. Biol. Fish.* 19:55-67.
- Stone, H. H., and B. M. Jessop.**  
1992. Seasonal distribution of river herring *Alosa pseudoharengus* and *A. aestivalis* off the Atlantic coast of Nova Scotia. *Fish. Bull.* 90:376-389.
- Swynnerton, G. H., and E. B. Worthington.**  
1940. Notes on the food of fish in Haweswater (Westmoorland). *J. Anim. Ecol.* 9:183-187.
- Vigerstad, T. J., and J. S. Cobb.**  
1978. Effects of predation by sea-run juvenile alewives (*Alosa pseudoharengus*) on the zooplankton community at Hamilton Reservoir, Rhode Island. *Estuaries* 1:36-45.
- Vinogradov, V. I.**  
1984. Food of silver hake, red hake and other fishes on Georges Bank and adjacent waters, 1968-74. *NAFO Sci. Counc. Studies* 7:87-94.
- Warshaw, S. J.**  
1972. Effects of alewives (*Alosa pseudoharengus*) on the zooplankton of Lake Warskopmic, Connecticut. *Limnol. Oceanogr.* 17:816-825.
- Wells, L.**  
1970. The effects of alewife predation on zooplankton in Lake Michigan. *Limnol. Oceanogr.* 15:556-565.
- Windell, J. T.**  
1978. Digestion and the daily ration of fishes. In T. Bagenal (ed.), *Fish production in fresh waters*, p. 227-254. Blackwell Scientific Publs., London, 365 p.